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REVERSAL OF ASYMMETRY OF CHELAE IN *CALAPPA*
WEBER, 1795 (DECAPODA: OXYSTOMATA)

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Examination of identified specimens of *Calappa* in the collections of the Smithsonian Institution indicates that the asymmetry of chelae may be reversed completely, presumably when both chelipeds are regenerated simultaneously following autotomy, or only partially, when only a single cheliped has been regenerated. Of 809 specimens, seven, or a little less than 1 percent, exhibit complete reversal and two specimens, partial reversal. These phenomena occur with equal frequency on males and females and occur rarely also on specimens of other genera in the Calappinae. Attributes of the affected specimens are described in detail and general criteria are presented whereby chelae whose asymmetry has been reversed due to regeneration can be recognized.

In each species of the pantropical and warm temperate marine crab *Calappa*, the proximal portions of the chelae are normally similar to one another in size, shape, proportions, and ornamentation. However, complex morphological features on the dactylus and fixed finger of the right chela render the chelae and their individual elements quite distinctive. Because the right and left chelae exhibit what may be called "handedness," they are customarily termed major and minor, respectively (see Fig. 1).

Recently, Shoup (1968) described in detail how the descending lobular projection on the dactylus and the complementing teeth on the propodus of the major chela are used to secure

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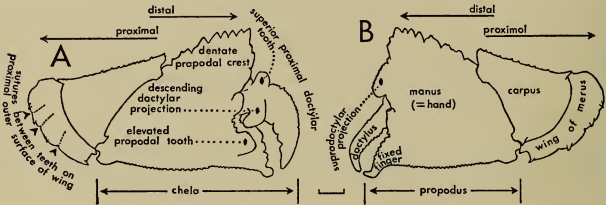


FIG. 1. Outline drawing of normal chelipeds (chela, carpi, and "wings" of meri) of *Calappa flammea* (Herbst), illustrating features and terminology cited in text. Elements are extended to their maximum, placing their outer surfaces approximately in the plane of the propodus. Bar scale represents 10 mm. A. Right major cheliped. B. Left minor cheliped.

food. An elevated tooth near the base of the fixed finger on the outer surface of the major propodus constitutes part of this apparatus and is usually extremely stout and conspicuous. This tooth is diagnostic of all species of *Calappa*, but published descriptions of the genus and its constituent species seldom attribute it specifically to either the right or left propodus. Alcock (1896: p. 140) and Rathbun (1937: p. 197) mentioned only that one propodus bears the tooth, but Barnard (1950: p. 347) noted that it is usually the right. Although varying in degree of expression, this tooth is also characteristic of the other Recent genera of the subfamily Calappinae, *Acanthocarpus* Stimpson, 1871, *Cycloes* de Haan, 1837, *Mursia* Demarest, 1823, and *Paracyclois* Miers, 1886.

While studying Eocene decapod remains from Florida, Ross, Lewis, and Sclaro (1964) encountered a unique right propodus which resembled the major propodus of a species of *Calappa* in shape and proportions, but which lacked any trace of the characteristic propodal tooth. Following a fruitless search of the literature and after consulting with workers having access to large collections of Recent species of *Calappa*, the authors concluded with some reservations that the fossil represented a new genus distinct from, but closely related to, *Calappa*. They realized, however, that the ultimate answer to the validity of the new genus rested in a thorough examination of large numbers of preserved specimens of *Calappa*.

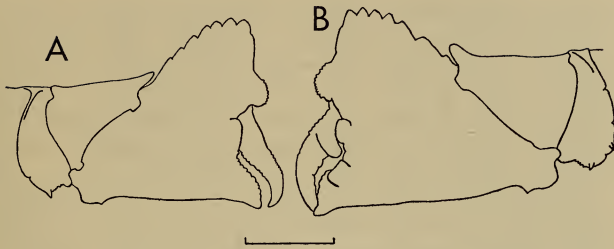


FIG. 2. Outline drawing of chelipeds of *Calappa hepatica* (Linné) (USNM 33400), illustrating complete and nearly perfect reversal of asymmetry. Elements are extended to their maximum, as in Fig. 1. Bar scale represents 10 mm. A. Right minor cheliped. Note smaller size relative to left cheliped, undefined teeth on wing of merus, and slightly abnormal proportions of propodus. B. Left major cheliped. Note poorly defined teeth on wing of merus, presence of supradactylar projection, and lack of superior proximal dactylar tooth.

The purpose of this paper is to report the results of such a study. A re-evaluation of the fossil genus in the light of these results appears in a separate note (Lewis, 1969).

OBSERVATIONS

Specifically, the problem under investigation is whether the distinctive characters of a minor chela do occur in species of *Calappa* on a right, customarily major, cheliped. In more general terms, is the asymmetry of the chelae ever reversed either partially (only one cheliped affected) or completely (both chelipeds affected)? These phenomena have not heretofore been discussed in the literature on these animals.

During the summer of 1967, the writer examined the variability of major and minor chelae on all identified specimens of *Calappa* in the alcoholic and dry collections of the Smithsonian Institution in order to determine (1) if reversal of asymmetry does occur; (2) if so, to what extent and under what circumstances; and (3) the variety and frequency of malformations which occur within the genus. Of the 809 specimens examined, 15 individuals possess conspicuously abnormal chelipeds. Of these, seven exhibit some degree of reversal of asym-

metry on both chelipeds, that is, complete reversal (see Table I and Fig. 2); two of seven other individuals exhibit partial reversal, and all seven of these specimens possess one completely normal cheliped and one abnormal cheliped which usually bears a grotesque propodus (see Table II); and one specimen shows the effects of injury to the propodus of one cheliped during normal growth (see Table II).

Considering in detail the characteristics of the left chelipeds of the specimens listed in Table I, the merus and carpus are quite indistinguishable from those of their unreversed counterparts, but in two cases [*C. hepatica* (Linné, 1758), USNM 33400 and 93819] the teeth on the wings of the meri are weakly delineated, although quite normal in number. Of appreciably greater significance among these specimens, the left (major) propodus usually retains a prominent supradactylar projection, which normally occurs only on the minor propodus, and the elevated tooth, which characteristically crowns the superior proximal margin of the major dactylus, is missing entirely on the left (major) dactylus (compare Figs. 1 and 2), as demonstrated by specimens of *C. flammea* (Herbst, 1794) (USNM 71113), *C. nitida* Holthuis, 1958 (USNM 103153), *C. hepatica* (USNM 33400), and *C. gallus* (Herbst, 1803) (USNM 48564). Partial exceptions are noted, however, on *C. hepatica* (USNM 93819), where both the supradactylar projection and the tooth are present, but the latter is strongly reduced, and on *C. ? flammea* (USNM 100833) and *C. gallus* (USNM 77211), on each of which the tooth and the supradactylar projection are absent.

The right chelipeds in this group of specimens are usually slightly smaller than the left, and their individual elements are dramatically more aberrant than those of the left. The teeth on the wings of the meri are universally fewer than normal in number and are usually weakly delineated; on one specimen of *C. hepatica* (USNM 33400), they are almost completely absent (see Fig. 2). However, the greatest divergence from normalcy lies in the shape and proportions of the right (minor) propodi and in the ornamentation on their outer surfaces. The propodi are almost as high as or higher than they

TABLE I. Smithsonian Institution specimens of *Calappa* exhibiting reversal of asymmetry of both chelae. Dimensions in millimeters; cl = carapace length, cb = carapace breadth (greatest width).

Species	Sex	USNM No.	Dimensions (mm.)		Locality	Comments
			cl	cb		
<i>C. flammea</i> (Herbst)	♀	71113	49.3	70.6	Puerto Colombia, Colombia	Chela of left cheliped rudimentary major; that of right minor, propodus abnormal in ornamentation.
<i>C. ? flammea</i> (Herbst)	y ♀	100833	17.9	22.2	Off Georgia	Chela of left cheliped near normal major; that of right minor, propodus abnormal in proportions and ornamentation.
<i>C. nitida</i> Holthuis	y ♀	103153	11.9	15.1	Surinam coast of South America	Same as immediately preceding.
<i>C. hepatica</i> (Linné)	♂	33400	36.1	60.1	Tari-Tari Island	Chela of left cheliped near normal major; that of right near normal minor.
<i>C. hepatica</i> (Linné)	♂	93819	35.2	57.3	Gilbert Islands	Same as immediately preceding.
<i>C. gallus</i> (Herbst)	y ♂	48564	17.0	20.6	Cuba	Chela of left cheliped near normal major; that of right minor, propodus abnormal in shape, proportions, and ornamentation.
<i>C. gallus</i> (Herbst)	♀	77211	41.0	54.0	No locality data	Chela of left cheliped near normal major; that of right minor, propodus abnormal in ornamentation.

TABLE II. Smithsonian Institution specimens of *Calappa* exhibiting one grotesque and/or reversed propodus. Dimensions in millimeters; cl = carapace length, cb = carapace breadth (greatest width). Symbols indicating kinds of abnormality: [RC] = single cheliped regenerated; [TC] = traumatized chela.

Species and Kind of Abnormality	Sex	USNM No.	Dimensions (mm)		Locality	Comments
			cl	cb		
<i>C. flammaea</i> (Herbst) [RC]	♂	66441	55.6	79.1	Key West, Florida	Chela of right cheliped normal major; that of left minor, propodus strongly abnormal in size, shape, proportions, and ornamentation.
<i>C. ocellata</i> Holthuis [RC]	♂	99990	65.5	95.8	Haiti	Same as immediately preceding.
<i>C. sulcata</i> Rathbun [RC]	♀	99980	46.2	65.4	Texas	Same as preceding.
<i>C. sulcata</i> Rathbun [RC]	♂	103450	57.6	73.3	Between British Guiana and Surinam	Chela of left cheliped normal minor; that of right minor, propodus strongly abnormal in shape, proportions, and ornamentation.
<i>C. sulcata</i> Rathbun [RC]	♀	103450	43.1	53.6	Between British Guiana and Surinam	Chela of right cheliped normal major; that of left minor, propodus slightly abnormal in size and ornamentation.

TABLE II (Cont'd.)

Species and Kind of Abnormality	Sex	USNM No.	Dimensions (mm)		Locality	Comments
			cl	cb		
<i>C. hepatica</i> (Linné) [RC]	♀	65355	29.6	41.9	Philippines	Chela of right cheliped normal major; that of left minor, strongly abnormal in size, shape, proportions, and ornamentation.
<i>C. hepatica</i> (Linné) [RC]	♂	99134	53.4	95.4	Oahu, Hawaii	Chela of left cheliped normal minor; that of right minor, strongly abnormal in size, shape, proportions, and ornamentation.
<i>C. hepatica</i> (Linné) [TC]	♂	65418	30.7	47.4	Philippines	Left cheliped normal; merus and carpus of right normal, but propodus traumatized and both elements of chela abnormal in shape, proportions, and ornamentation.

are long on *C. ? flammea* (USNM 100833), *C. nitida* (USNM 103153), *C. hepatica* (USNM 33400), and *C. gallus* (USNM 48564). Usually, surface ornamentation is sparse and diverges to varying degrees from the typical. Tuberculation is generally weak, uneven, and random rather than orderly (*C. flammea*, USNM 71113; *C. ? flammea*, USNM 100833; and *C. gallus*, USNM 48564), and granulation, also typically sparse and random, may be lacking almost entirely (*C. flammea*, USNM 71113). On *C. nitida* (USNM 103153), there is little difference in size between tubercles and granules; on *C. gallus* (USNM 48564), tubercles are really random, completely hairless, overgrown granules totally unlike the customary diagnostic laminae; on *C. gallus* (USNM 77211), the tubercles are strong and sharp or distinctly peglike. In general, surface ornamentation on these propodi is conspicuously sparse, and large portions are smooth, or nearly so, with occasional randomly distributed tubercles and patches of granules. Exceptions are the two specimens of *C. hepatica* (USNM 33400 and 93819), on which ornamentation is virtually indistinguishable from that on normal propodi; on the former specimen, tuberculation is weaker on the right than on the left propodus, but less pronounced variations in strength of ornamentation on opposing propodi were observed occasionally among otherwise normal specimens of all species of *Calappa* examined in this study.

The first seven specimens listed in Table II, marked "[RC]," indicate that when only one cheliped is abnormal, the affected appendage is invariably small and/or grotesque, and, with a single partial exception, the propodus is conspicuously aberrant in shape, proportions, and ornamentation. Five of these specimens exhibit the characteristics of a minor appendage on the left cheliped (*C. flammea*, USNM 66441; *C. ocellata* Holthuis, 1958, USNM 99990; *C. sulcata* Rathbun, 1898, USNM 99980, and the female, USNM 103450; and *C. hepatica*, USNM 65355). On four, the teeth on the wings of the left meri are fewer than normal in number, and, where well delineated, they bear peculiar, atypical terminations; the superior crests on the left propodi of *C. flammea* (USNM 66441) and *C. ocellata* (USNM 99990) bear far more than the normal number of

teeth and the crest on *C. hepatica* (USNM 65355) is rounded and bumpy, lacking completely any trace of teeth; and the outer surfaces of the left propodi are generally smooth with ornamentation confined to a few, knobby, often random tubercles. The female *C. sulcata* (USNM 103450) represents the partial exception mentioned above. Like the four specimens just discussed, its abnormal left cheliped bears a minor chela, but, unlike them, the teeth on the wing of the left merus are normal; ornamentation on all parts of the left cheliped is almost normal also, but all elements are small and in life they were evidently atypically colored, the color in alcohol being grayish purple, in marked contrast to the cream to ivory-colored elements of the right cheliped.

The remaining two specimens in this group have characteristics of a minor appendage on the right cheliped and thereby exhibit partial reversal. The wing of the right merus on the male *C. sulcata* (USNM 103450) has five teeth which are strongly hooked distally, and that of *C. hepatica* (USNM 99134) has only two unusual quadrate teeth. In proportions, relative size, and ornamentation, the right propodi of these specimens resemble the strongly aberrant left propodi on the four other members of this group discussed earlier.

The only abnormality observed during this study which was caused solely by injury during normal growth occurs on *C. hepatica* (USNM 65418), listed last and marked "[TC]" in Table II. The left cheliped is normal, as are the right merus and carpus. However, the inferior margin and the lower part of the outer surface of the right (major) propodus were apparently slashed or constricted distally, and although the wound healed completely, a depressed scar remains, the distal proportions of the chela are strongly altered, and ornamentation on the outer surface of the propodus is confined to small, sharp, scattered projections. Also, extension is restricted between carpus and propodus due to incompletely developed hinges.

DISCUSSION

Reversed asymmetry of chelipeds has been described for some ocypodid brachyurans, alpheid shrimp, and nephropid

macrurans. Details of reversal vary from group to group, but perhaps the strongest contrast to the reversal in *Calappa* is Herrick's (1907) account of the approximately equal frequency of complete and perfect reversal of asymmetry on chelae of the American lobster, *Homarus americanus* H. Milne-Edwards, 1837. Herrick (1907, p. 275) indicated that handedness on these animals is a genetically controlled, inherently variable but not random character, and stated that "this condition is probably one of direct inheritance, all members of a brood being either right-handed or left-handed," the position of the major ("crushing" or "club") and minor ("toothed" or "quick") chelae being "predetermined in the egg."

Whereas reversal may be frequent, complete, and perfect on lobsters, it is infrequent and imperfect on specimens of *Calappa*. Because features unlike those normally observed on unreversed chelipeds occur on the individual elements of reversed chelipeds, complete reversal in these crabs is attributed here to simultaneous and equal or near-equal regeneration of both chelipeds following autotomy. In support of this interpretation, it should be noted that these appendages are almost equal in size but are generally slightly smaller than their normal, unreversed counterparts, and their individual elements are more or less correctly proportioned relative to one another but, again, are somewhat smaller than their unreversed counterparts.

Thus, when both chelipeds are lost on specimens of *Calappa*, their asymmetry may be reversed completely during subsequent regeneration, and occurrence of this phenomenon is not confined to either sex; if examined only superficially, the left cheliped usually appears almost perfectly formed, but the right is generally malformed in several respects, most noticeably in size and in the characteristics of the wing of the merus and the proportions and ornamentation of the propodus. Truly near-perfect reversal of the asymmetry of chelae was observed only on *C. hepatica* (USNM 93819), but even this specimen lacks some, albeit minor, features on its chelipeds which are diagnostic of a normal, unreversed condition.

It may be significant that when only one cheliped is lost, the attributes of the replacement chela are apparently never

those associated with the original major chelipeds. Regardless of which cheliped is autotomized, the plan of the regenerated appendage seems to be the simpler of the two possible alternatives, but one should probably not attach phylogenetic significance to this observation, especially since at present the genetic and/or biochemical mechanisms whereby the characteristics of replacement appendages are determined are so poorly understood.

Regarding general ramifications of this study, it is suggested that autotomy and subsequent regeneration of chelipeds among Recent species of *Calappa* is comparatively uncommon, partly because their digging or burrowing habit affords the animals considerable initial protection, but primarily because the posterolateral clypeiform expansions and the characteristic posture with which the chelipeds are carried, closely appressed to the frontal and anterolateral margins of the carapace, probably provide the most effective protection to these appendages which is to be seen among all brachyurans. This is not to imply that the animals are rendered impregnable by their tanklike attributes, as three specimens of *C. flammea* (USNM 5233), taken in 1883 from fish stomachs off Pensacola, Florida, demonstrate conclusively that species of *Calappa* are preyed upon by marine vertebrates. However, because the chelipeds are needed to secure food and, at the same time, form an indispensable part of an elaborate respiratory apparatus necessarily associated with the animals' normally buried or partially buried existence (see Garstang, 1897), it is likely that, following loss of these appendages, few individuals survive long enough to regenerate new chelipeds.

Because reversal is apparently associated only with regeneration, it appears that under all normal conditions the major chela in *Calappa* occurs only on the right cheliped and that this character is probably ancient, well established, and strongly maintained genetically. As reversal *per se* is presumably neither advantageous nor disadvantageous to an individual, its survival value is probably negligible so long as one cheliped possesses the unusual characteristics of a major chela in perfect working order. The two specimens whose major chelae were

not fully functional (*C. flammea*, USNM 71113 and *C. hepatica*, USNM 65418) probably experienced difficulty in feeding using the techniques described by Shoup (1968). However, the two individuals which exhibit partial reversal and lack major chelae on both chelipeds (the male *C. sulcata*, USNM 103450 and *C. hepatica*, USNM 99134) were certainly prevented from feeding in their characteristic manner on their preferred diet of gastropods and to have survived, they must have altered their feeding habits considerably.

This study was concerned initially only with species of *Calappa*, but chelae reversed according to the previously noted general rules occur also in species of other calappid genera. Reversal is complete and nearly perfect on a male specimen of *Cycloes bairdii* Stimpson, 1860, collected off Sao Luís, Brazil, in 1963 (USNM 123339); both chelipeds are similar in size, shape, proportions, and ornamentation, but where only the minor (left) propodus customarily bears a stout supradactylar projection in this species, strong projections are present on both major (left) and minor (right) propodi of this individual. In addition, the entire right cheliped has been regenerated on a large male specimen of *Mursia gaudichaudii* (H. Milne-Edwards, 1837), collected in 1966 northwest of Valparaiso, Chile (USNM 123610), and the right (minor) propodus is conspicuously small and atypical in both proportions and ornamentation. Finally, a single, isolated right chela (USNM 77170), clearly assignable to *Acanthocarpus alexandri* Stimpson, 1871, and collected in 1930 south of the Tortugas, Florida, was regenerated grotesquely as a minor chela. Thus, complete and partial reversals evidently occur throughout the Calappinae, but judging from the small percentage of specimens of *Calappa* which exhibited reversed chelae, these phenomena are probably not widespread within either a population or any given species.

Reports of reversal in *Calappa* are rare in the literature and where they exist, they are brief statements without detailed descriptions or discussion. Holthuis (1958: p. 172) cited a probable case of partial reversal on a male specimen of the Caribbean species *C. cinerea* Holthuis, 1958, from St. Martin,

Netherlands Antilles. The right chela he described as "very small and of abnormal shape, somewhat resembling the small [left] chela," concluding, "It is evidently in process of regeneration."

The only other report of reversal known to the writer is that by Barnard (1950: p. 347), who mentioned having seen "two 'sinistra' specimens in 20 specimens" of *C. hepatica spinosissima* H. Milne-Edwards, 1837. Barnard did not specify whether reversal on these specimens is complete or partial, although by noting this occurrence in the same short footnote with comments concerning the seemingly perfect reversal on Miers' (1886) plates of the "Challenger" brachyurans, he implied that reversal on these specimens is complete. If this was indeed his intention, the 10 percent reversal reported for *C. hepatica spinosissima* represents a significantly greater frequency than that observed on specimens in the Smithsonian collections, in which slightly less than 1 percent of all specimens are thus affected. Of the 172 specimens of *C. hepatica* examined, only two, or a little over 1 percent, have completely reversed chelae, and neither of the two specimens of *C. hepatica spinosissima* exhibits reversal. Therefore, either the specimens studied by the writer do not accurately reflect the frequency of the phenomenon in nature, or Barnard's samples were atypical, or complete reversal is unusually common within this subspecies, at least from this geographic area. It is impossible to determine which, if any, of these alternatives is correct, but because of its diversity and large numbers of individuals, the material in the Smithsonian collections is considered fairly representative of the genus.

Regarding the apparent reversal in Miers' (1886) illustrations of the chelae of *C. flammea* (pl. 23, fig. 1b) and *C. depressa* Miers, 1886 (pl. 23, fig. 2b), Barnard (1950: p. 347) observed that these figures "may be mirror-pictures due to reversal in the lithographing process." That Barnard was probably quite correct is indicated by the total lack of comment concerning reversal in Miers' text; had any of the "Challenger" specimens exhibited such an unusual phenomenon, it is extremely unlikely that Miers would have failed to mention it.

Indeed, Miers' illustrations of the chelae of *Paracyclois milne-edwardsii* Miers, 1886 (pl. 24, fig. 1c), and *Mursia curtispina* Miers, 1886 (pl. 24, fig. 2c), likewise representatives of the Calappinae, also show apparent reversal, but again no relevant comments appear in the text.

One of the lithographs of *Calappa granulata* (Linné, 1758), executed by Roux (1828), shows chelae apparently reversed (pl. 2, fig. 1), but another in the same work shows them in unreversed position (pl. 16, figs. 1, 3-4). The excellent detail in the former indicates that in size and proportions, at least, these elements are quite normal, but, as in Miers (1886), there is no mention of reversal or variability in handedness in the text, and this is probably another example of error attributable to the lithographing process.

SUMMARY AND CONCLUSIONS

In the Calappinae, major chelae bearing specialized structures normally occur on the right chelipeds and minor chelae, lacking these structures, on the left. To investigate the existence, frequency, and significance of reversed asymmetry of chelae in Recent species of *Calappa* and to assess the degree of variability and malformation of their chelipeds, the writer examined 809 identified specimens in the collections of the Smithsonian Institution and found 15 with abnormal chelipeds.

Complete reversal of asymmetry was observed on both chelipeds of seven specimens, and in these cases, reversal is attributed to simultaneous and approximately equal regeneration of these appendages following autotomy rather than to any inherent genetic causes. Features which usually occur only on completely reversed chelipeds and differ from those on normal, unreversed chelipeds include the following: (1) on both chelipeds: smaller than normal size, relative to size of carapace and other appendages; (2) on left (major) chelipeds: (a) retention of all or part of supradactylar projection on propodus, and (b) virtual absence of elevated tooth on superior proximal margin of dactylus; and (3) on right (minor) chelipeds: (a) smaller size of entire chelipeds and individual elements, relative to left counterparts and to minor cheliped on unreversed specimens, (b) reduced number of teeth on wing of merus,

strength and delineation of individual teeth being generally weak and overall appearance of wing aberrant, (c) atypical shape and proportions of propodus, and (d) paucity of characteristic ornamentation on outer surfaces of all elements, especially on propodus, where occasional random tubercles and patches of granules occur on otherwise smooth surface. These characters apply well to all seven reversed specimens except in the ornamentation and proportions of the right (minor) propodi on two specimens of *C. hepatica* which exhibit almost perfect reversal.

When only one cheliped is regenerated, the plan of the replacement chela is apparently always that of the minor, more generalized chela, regardless of whether it is produced on the left or right appendage; if on the latter, the condition constitutes partially reversed asymmetry. Features exhibited on seven specimens, characteristic of regeneration of only a single cheliped, include: (1) quite normal size, shape, proportions, and ornamentation of unregenerated cheliped and its elements, in contrast to markedly smaller size and deviations in shape, proportions, and ornamentation of regenerated limb and its parts, (2) reduced number and atypical ornamentation of teeth on wing of regenerated merus, (3) strongly aberrant shape and proportions of regenerated propodus, (4) generally smooth outer surface of propodus, with few, knobby, usually randomly distributed tubercles, and (5) unusual characteristics of superior crest of propodus, either dentate with an excessive number of teeth or rounded with no teeth at all.

The one injured specimen which the writer encountered suggests that when an element of a cheliped is damaged, the wound may affect subsequent growth and the involved part may become conspicuously atypical and, depending on the extent of the injury, even grotesque. However, the abnormality is generally confined to that particular element and, therefore, the condition is easily recognized.

With the demonstration of complete and partial reversal of asymmetry of chelae in species of the Calappinae, it becomes obvious that ordinarily no taxonomic significance can be attached to the attributes of reversed or injured chelae on speci-

mens otherwise clearly assignable to this subfamily. Because the fossil propodus mentioned earlier probably represents a case of complete and nearly perfect reversal, it may represent an exception to the generalization just stated, and its attributes may be taxonomically significant at the specific level. Consequently, the type-species of the fossil genus recognized by Ross, Lewis, and Scolaro (1964) should probably be reassigned to the genus *Calappa*, with which it has its closest affinities.

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